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DARWIN'S CONTRIBUTION TO THE KNOWLEDGE OF HYBRIDIZATION

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THE period from 1859 until the re-discovery of Mendel's papers in 1900 was so strongly colored by the views of Charles Darwin, and so dominated by the magnitude of his work, that it sometimes seems as though originality and initiative had been abandoned, and as though, so far as evolution were concerned, the scientific world had remained content simply to quote Darwin.

It is the purpose of the present paper to present the contributions of Darwin to the knowledge of hybrids. To this end it seems desirable, so far as possible, to let Darwin's words speak for themselves, and hence, although the paper may seem burdened with extracts, yet, for those interested in tracing the history of ideas in genetics, it will perhaps be of service to assemble such a résumé of Darwin's work and thought in the field of hybridization. Brought together in such a way, an author's contribution may be more successfully valuated at leisure by those who may be interested. The writer has, therefore, sought to bring together, in somewhat connected and coherent form, the various views, conclusions and experimental data on the subject of hybrids and hybridization, found in Darwin's different writings.

It is also the purpose of the writer to bring into relief certain fields of investigation opened by him, but in which, so far as appears, there has been little or no research since his time.

On November 24, 1859, appeared the first edition of "The Origin of Species (1), antedating by seven years, the appearance of the papers of Mendel.

One of the primary questions concerning crossing that interested Darwin was the matter of sterility and fertility in hybrids. Investigators before Darwin's time had been to a considerable extent obsessed by the species question, which crossing was supposed to solve. If a cross succeeded, or produced fertile offspring, it argued that the parent forms were "varieties." If the cross failed, or if its offspring were sterile, it demonstrated that they were "species." With the sole exception of Sageret (2), none of the earlier hybridists seems to have formed anything like the unit-character conception, and with the sole exception of Naudin and Darwin, no scientific theory was conceived of which might explain the *modus operandi* of amphimixis in the case of hybrids.

By Darwin, the question of hybridization, while indeed for the most part, taken up more or less conventionally, received, nevertheless, broader treatment. To begin with, Darwin held that the inability of species to cross "is often completely independent of their systematic affinity, that is, of any difference in their structure or constitution, excepting their reproductive systems" (1a, 2:14).

So that, even as early as the writing of the "Origin of Species," Darwin is seen to maintain that the susceptibility of plants to crossing stood in no relation to the degree of their resemblance to either parent, and that "the facility of making a first cross between any two species is not always governed by their systematic affinity or degree of resemblance to each other" (1a, 2:16).

This fact, he adds, is demonstrated by the case of reciprocal crosses, alluding here to the relative facility of making the cross, according as the one or the other species is used as the male or the female.

Occasionally he says there is "the widest possible difference in the facility of effecting a union. The hybrids, moreover, produced from reciprocal crosses, often differ in fertility" (*ibid.*).

Darwin again later in "Animals and Plants under Domestication," refers to the matter as follows:

> Why should some species cross with facility, and yet produce very sterile hybrids, and other species cross with extreme difficulty, and yet produce fairly fertile hybrids? Why should there often be so great a difference in the result of a reciprocal cross between the same two species? (1a, 2:17).

Darwin comments frequently in the "Origin of Species," upon the fact that the hybrids produced from reciprocal crosses often differ in fertility, and that while two species may be difficult to cross, there is no strict parallelism between the difficulty of effecting the cross and the degree of sterility of the hybrids resulting therefrom.

As Darwin observes, differences in the results in respect to the relative ease of making reciprocal crosses had been previously noted by Koelreuter, who found, after two hundred trials, continued for eight years, that while *Mirabilis jalapa* could easily be fertilized by *M. longiflora,* the reverse cross could not be effected.

With regard to the difference in the facility with which reciprocal crosses can be made, there may be some fundamental resemblance between this fact and the ease with which reciprocal grafts can be made, wherein Darwin instances the fact that the currant can, although with difficulty, be grafted upon the gooseberry, while the reciprocal graft can not be made. Certainly the well-established facts of somatic segregation followed by germinal "mutation"—so-called, should sufficiently indicate that the behavior of the somatic and of the reproductive cells should not be regarded as being so sharply separated as is usually done in genetic studies. At all events, the problem as to the reason for the relative differences in the respective facility of making reciprocal crosses, as well as the further one of the differences as in the case of mule and hinny, between the respective products of reciprocal crosses, are questions that have been but very little investigated since Darwin's time, and demand thorough exploration.

Since the advent of Mendelian studies in 1900, it has been rather conventionally and very loosely assumed that reciprocal crosses are invariably identical in type. That such is not necessarily the case, Darwin's early observations should suffice to indicate.

The problem of the fertility of selfed and crossed plants engaged Darwin's close interest in forty-one cases belonging to twenty-three species. The ratio of the fertility of the crossed to that of the self-fertilized plants was found to be as 100:60. In another experiment to determine the relative fertility of flowers when crossed or selfed, the ratio in thirty cases belonging to twenty-seven species was as 100:55.

> There is no evidence, Darwin finds, That the fertility of plants goes on diminishing in successive self-fertilized generations, and no close correspondence, either in the parent plants or in the successive generations, between the relative number of seeds produced by the crossed and self-fertilized flowers, and the relative powers of growth of the seedlings raised from such seeds (1b, 327).

Darwin's investigations were directed quite extensively to the question of self-fertility in plants, a field which bears strongly upon our knowledge of heredity, but in which likewise comparatively little experimental work has been done since his time. As the result of his own studies, supplemented by those of Hildebrand and Fritz Müller, he was able to say:

> We may therefore confidently assert, that a self-sterile plant can be fertilized by the pollen out of any one out of a thousand or ten thousand individuals of the same species, but not by its own (*ibid.*, 347).

Regarding the cause of sterility or inability to accept fertilization, we are as greatly at a loss for an explanation to-day as was Darwin. As Darwin well states it:

> The veil of secrecy is as yet far from lifted; nor will it be, until we can say why it is beneficial that the sexual elements should be differentiated to a certain extent, and why, if the differentiation be carried still further, inquiry follows. It is an extraordinary fact that with many species, flowers fertilized with their pollen are either absolutely

> or in some degree sterile; if fertilized with pollen from another flower on the same plant, they are sometimes, though rarely, a little more fertile; if fertilized with pollen from another individual or variety of the same species they are fully fertile; but if with pollen from a distant species they are sterile in all possible degrees, until utter sterility is reached. We thus have a long series with absolute sterility at the two ends; at one end due to the sexual elements not having been differentiated, and at the other end to their having been differentiated in too great a degree, or in some peculiar manner (*ibid.*, 455).

The questions which Darwin raises in this connection are as follows (p. 458):

1. Why the individuals of some species profit greatly, others very little by being crossed.
2. Why the advantages from crossing now seem to accrue exclusively to the vegetative and now to the reproductive system, although generally to both.
3. Why some members of a species should be sterile, while others are entirely fertile with their own pollen.
4. Why a change of environment or of climate should affect the sterility of self-sterile species.
5. Why the members of some species should be more fertile with the pollen from another species than with that of their own.

Regarding the general matter of sterility in hybrids, Darwin comments as follows:

> It is notorious that when distinct species of plants are crossed they produce with the rarest exceptions, fewer seeds than the normal number. This unproductiveness varies in different species up to sterility so complete that not even an empty capsule is formed (1b, 463).
>
> It is also notorious that not only the parent species, but the hybrids raised from them are more or less sterile, and that their pollen is in a more or less aborted condition. The degree of sterility of various hybrids does not always strictly correspond with the degree of difficulty in uniting the parent forms. When hybrids are capable of breeding *inter se,* their descendants are more or less sterile, and they often become still more sterile in the later generations (*ibid.*).
>
> With the majority of species, flowers fertilized with their own pollen yield fewer, sometimes much fewer seeds, than those fertilized from another individual or variety (*ibid.*, 464).

As the result of his investigations regarding sterility to pollen, Darwin was able to render at least one service, that of removing the obsession which had so long afflicted the study of the hybrid question, viz., the variety-species discussion. He says:

> It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties. The evidence from this source graduates away and is doubtful in the same degree as is the evidence derived from other constitutional and structural differences (1a, 2:4).

The question of the chemical and cytological basis for sterility or non-receptivity to pollen, remains still in part an open field for the investigator.

One of the most important questions from our present-day point of view which Darwin investigated was the relative vigor of first-generation hybrids as compared with that of their parents. The following allusions occur in the "Origin of Species."

Darwin comments on the fact that crosses between individuals of the same species, where they differ to a certain extent, give increased vigor and fertility, while close fertilization, long continued, almost always leads to physical degeneracy, and remarks:

> We know also that a cross between the distinct individuals of the same variety, and between distinct varieties, increases the number of the offspring, and certainly gives to them increased size and vigor (1a, 2:296).

Darwin thoroughly investigated, as is well known, the comparative relation of the offspring of crossed to those of selfed plants with respect to vigor.

> I have made so many experiments, and collected so many facts, showing on the one hand that an occasional cross with a distinct individual or variety increases the vigor and fertility of the offspring, and on the other hand that very close interbreeding lessens their vigor and fertility, that I can not doubt the correctness of this conclusion (2a, 2:5).

> Again, from both plants and animals, there is the clearest evidence that a cross between individuals of the same species, which differs to a certain extent, gives vigor and fertility to the offspring, and that close interbreeding, continued during several generations between the nearest relations, if these be kept under the same conditions of life, almost always leads to decreased size, weakness or sterility (1a, 2: 27).

In "Cross and Self Fertilization," Darwin again discusses the effects of crossing as follows, expressing the view:

> Firstly, that the advantages of cross-fertilization do not follow from some mysterious virtue in the mere union of two distinct individuals, but from such individuals having been subjected during previous generations to different conditions, or to their having varied in a manner commonly called spontaneous, so that in either case their sexual elements have been in some degree differentiated; and secondly from the want of such differentiation in the sexual elements (1b, 443).
>
> A cross with a fresh stock or with another variety seems to be always beneficial, whether or not the mother plants have been intercrossed or self-fertilized for several previous generations (1b, 444).

Darwin also remarks upon the greater power of the cross-fertilized plants in his experiment to stand exposure, the crossed plants enduring sudden removal from greenhouse to out-of-door conditions better than did the self-fertilized, and also resisting cold and intemperate weather conditions more successfully. This was the case with morning glory and with *Mimulus*.

> The offspring of plants of the eight self-fertilized generations of *Mimulus* crossed by a fresh stock, survived a frost which killed every single self-fertilized and intercrossed plant of the old stock.
>
> Independently of any external cause which could be detected, the self-fertilized plants were more liable to premature death than the crossed (*ibid.*, 290).

Out of several hundred plants in all involved in the experiment, only seven of the crossed plants died, while at least twenty-nine of the self-fertilized were thus lost.

With regard to time of flowering, in four out of fiftyeight cases, a crossed plant, in nine cases a selfed plant, flowered first.

Darwin broached the view that the increased vigor of first-generation hybrids was chiefly due to the forms used in the cross having been exposed to somewhat different conditions of life. He also contended that his experiments proved that

> If all the individuals of the same variety be subjected during several generations to the same conditions, the good derived from crossing is often much diminished or wholly disappears (1a, 2:270).

This statement appears to be an *obiter dictum* of Darwin's to the support of which he does not adduce direct experimental evidence.

Again he says:

> Anyhow my experiments indicate that crossing plants which have been long subjected to almost though not quite the same conditions, is the most powerful of all the means for retaining some degree of differentiation in the sexual elements, as shown by the superiority in the later generations, of the intercrossed over the self-fertilized seedlings (1b, 450).
>
> We know, he says, that a plant propagated for some generations in another garden in the same district serves as a first stock, and has high fertilization powers (*ibid.*).

The importance of this view has yet, so far as the writer knows, to be thoroughly re-investigated under completely controlled conditions.

It was Darwin's view, as the result of his experiments, that the increased vigor of intercrossed plants is due to the constitution or nature of the sexual elements, which condition he took to be of the general nature of differentiation due to the action of environment.

> It is certain, he says, that the differences are not of an external nature, for two plants which resemble each other as closely as the individuals of the same species ever do, profit in the plainest manner when intercrossed, if their progenitors have been exposed during several generations to different conditions (1b, 270).

Darwin asserts that there is not a single case in his experiments,

> Which affords decisive evidence against the rule, that a cross between plants, the progenitors of which have been subjected to somewhat diversified conditions, is beneficial to the offspring (*ibid.,* 281).

The fact that increased vegetative vigor in first generation hybrids was also sometimes accompanied by diminished fertility was likewise observed by Darwin,

> For it deserves especial attention that mongrel animals and plants, which are so far from being sterile, that their fertility is often actually augmented, have, as previously shown, their size, hardiness and constitutional vigor generally increased. It is not a little remarkable that an accession of vigor and size should thus arise under the opposite contingencies of increased and diminished fertility (1c, 2: 108).

In the case of Darwin's experiments to determine the relative effects upon vigor of selfing and crossing, respectively, the data were determined chiefly with respect to height and weight of the plants, which were grown on opposite sides of the same pot in all instances.

Regarding the relative heights and weights of 292 plants, derived from a cross with a fresh stock, and of 305 plants either selfed or intercrossed, between plants of the same stock and belonging to thirteen species and twelve genera, Darwin says:

> Considering all the cases . . . there can be no doubt that plants profit immensely, though in different ways, by a cross with a fresh stock, or with a distinct sub-variety. He emphasizes further, It can not be maintained that the benefit thus derived is due merely to the plants of the fresh stock being perfectly healthy, whilst those which had been long intercrossed or self-fertilized had become unhealthy; for in most cases there was no appearance of such unhealthiness (1b, 269).

Experiments were also made with plants belonging to five genera in four different families. One of the most interesting cases was that of a plant of marjoram (*Origanum vulgare*). The height of the crossed was to that of the selfed plants as 100:86.

> They differed also to a wonderful degree in constitutional vigor. The crossed plants flowered first, and produced twice as many flower-stems; and they afterward increased by stolons to such an extent as almost to overwhelm the self-fertilized plants (1b, 302).

Darwin holds that the inferiority of the selfed seedlings in height can have been in no way due to any morbidity or disease in the mother plants; certainly, he maintains, no such theory of a diseased condition would in any wise hold, in the case of

> intercrossing the individuals of the same variety or of distinct varieties, if these have been subjected during some generations to different conditions (1b, 445).

In four out of the five cases experimented with, the intercrossing of flowers upon the same plant did not differ in effect from the strictest self-fertilization. Concluding, he says:

> On the whole the results here arrived at . . . agree well with our general conclusion, that the advantage of a cross depends on the progenitors of the crossed plants possessing somewhat different constitutions, either from having been exposed to different conditions, or to their having varied from unknown causes in a manner which we in our ignorance are forced to speak of as spontaneous (1b, 302).

Darwin's experiments indicated as in the case of heartsease and sweet pea, that

> the advantage derived from a cross between two plants was not confined to the offspring of the first generation (1b, 305).

Laxton's varieties of sweet peas produced by crossing, as Darwin says:

> have retained their astonishing vigor and luxuriance for a considerable number of generations (*ibid.*).

Darwin concludes:

> As the advantage from a cross depends on the plants which are crossed differing somewhat in constitution, it may be inferred as prob-

> able that under similar conditions, a cross between the nearest relations would not benefit the offspring so much as one between non-related plants (*ibid.*).

Darwin finally also remarks in general:

> It is interesting to observe . . . the graduated series from plants which, when fertilized by their own pollen, yield the full number of seeds, but with the seedlings a little dwarfed in stature, to plants which, when self-fertilized, yield few seeds, to those which yield none, but have their ovaria somewhat developed,—and, lastly, to those in which the plant's own pollen and stigma mutually act on one another like poison (.lc, 2: 119).

The relative weight and germinative energy of seeds from crossed and from self-fertilized plants, was investigated by Darwin in the case of sixteen species, with the result that the weight of the seeds of the former to that of the latter was found on the average to be as 100:96. In ten out of the sixteen cases the self-fertilized seeds were either equal or superior to the crossed in weight, but in six out of these ten, the plants raised from these selfed seeds were greatly superior in height and in other respects to those from the crossed seeds. In the matter of germination of selfed and crossed seeds, the results were conflicting. Darwin, however, discovered that, in general, seedlings of greater constitutional vigor are obtained when crossed by other individuals of the same stock, than when pollinated by their own pollen.

In the cases of plants of fifty-seven different species, belonging in all to fifty-two genera and thirty different families, Darwin carried out the most extensive experiment yet recorded, conducted for the purpose of determining the differences in size, between the offspring of cross-fertilized and of close-fertilized plants.

The total number of the crossed plants amounted to 1101, and of the selfed plants to 1076. As a result, Darwin found that the plants derived from crosses between different strains of the same species, were taller on the average, than plants derived from crosses within the same strain, and taller in the latter case than in the case of the offspring of self-fertilized plants. The average ratio of 620 crossed to 607 selfed plants in height, derived from Darwin's tables, was as 100:86.

From the fact that flower buds are in a sense distinct individual plant units, which sometimes vary and differ widely from one another, and yet, when on the same plant, owing to the fact that the plant has come from the same fertilized cell, rarely are widely differentiated, Darwin reasons that the effects of intercrossing can be explained. He says:

> The fact that a cross between two flowers on the same plant does no good or very little good, is likewise a strong corroboration of our conclusion; for the sexual elements in the flowers on the same plant can rarely have been differentiated, though this is possible, as flower buds are in one sense distinct individuals, sometimes varying and differing from one another in structure or constitution (1b, 444).

Hence, he concludes:

> Thus the proposition 'that the benefit from cross-fertilization depends on the plants which are crossed having been subjected to somewhat different conditions, or to their having varied from some unknown cause as if they had been thus subjected, is securely fortified from all sides (1b, 444).

Darwin comments also on the reversed situation, where changes in the external condition result in sterility, for which he seeks to find a logical connection with the condition induced by crossing.

> On the one hand, slight changes in the conditions of life are favorable to plants and animals, and the crossing of varieties adds to the size, vigor, and fertility of their offspring, so on the other hand, certain other changes in the conditions of life cause sterility; and as this likewise ensues from crossing much modified forms or species, we have a parallel and a double series of facts, which apparently stand in close relation to each other (1c, 2:126).

Darwin's view as to the reason for the good effects of crossing was based upon the long prevalent opinion that, since animals, and hence presumably plants, profit from changes in their conditions, that probably such changes operate to affect the germ cells, or that in some way the germ cells receive an extra stimulation on that account, which redounds to the benefit of the offspring (1c, 2:155).

Darwin appears to hold the ill effects of close fertilization to be due to the fact that the sexual elements in the different flowers on the same plant have not differentiated, while in his conclusion he appears to consider the benefits of cross-fertilization to be due to the individuals involved in the cross having differentiated through having been exposed to different conditions.

Darwin frequently emphasizes the same view regarding the differentiating effects of a new environment.

> But hardly any cases afford more striking evidence how powerfully a change in the conditions of life acts on the sexual elements, than those already given, of plants which are completely self-sterile in one country, and when brought to another, yield even in the first generation, a fair supply of self-fertilized seeds (1b, 477), and again, . . . we know that a plant propagated for some generations in another garden in the same district scores as a fresh stock and has high fertilizing powers. The curious cases of plants which can fertilize and be fertilized by any other individual of the same species but are altogether sterile with their own pollen, become intelligible, if the view here propounded is correct, namely, that the individuals of the same species, growing in a state of Nature near, have not really been subjected during several previous generations to quite the same conditions (1b, 450).

> When two varieties which present well-marked differences are crossed, their descendants in the later generations differ greatly from one another in external characters; and this is due to the augmentation or obliteration of some of these characters, and to the reappearance of former ones through reversion; and so it will be, as we may feel almost sure, with any slight differences in the constitution of their sexual elements (1b, 449).

With regard to the ill effects derived from self-fertilization, Darwin says:

> Whether the evil from self-fertilization goes on increasing during successive generations is not as yet known, but we may infer from my

> experiments that the increase, if any, is far from rapid. *After plants have been propagated by self-fertilization for several generations, a single cross with a fresh stock restores their pristine vigor,* and we have a strictly analogous result with our domestic animals. The good effects of cross fertilization are transmitted by plants to the next generation, and judging from the varieties of the common pea, to many succeeding generations. But this may merely be that crossed plants of the first generation are extremely vigorous, and transmit their vigor like any other character to their successors (1b, 438).

In this paragraph Darwin calls attention to a fact that attracted little attention for a generation,—viz., the immediate improvement due to a cross. Darwin was thus if not the first to call sharply to attention, the matter of the relatively increased size and vigor of first generation hybrids, at least the first to subject the question to experimental analysis.

So far as plant hybrids are concerned, Darwin's mind was chiefly occupied, as we have seen, not so much with the fundamental theory of hybrids, as with the question of sterility in hybrids and its inheritance. The general question of what is the essential nature of hybridity, and how and in what manner the characters are distributed in the hybrid offspring, seems not to have come to an issue with him.

However, among the matters of interest to modern students of genetics are his recognition of the general fact of the intermediacy of F_1 hybrids, and of the occasional complete dominance of one or the other set of parental characters, together with the phenomena which he terms "reversion." Regarding the former matter he remarks:

> There are certain hybrids which, instead of having, as is usual, an intermediate character between their two parents, always closely resemble one of them (1, 2:15).

In regard to the behavior of characters in crosses, while admitting that, in the majority of cases, the hybrid offspring are intermediate between their parents, he recognized that certain characters are incapable of fusion.

> When two breeds are crossed, their characters usually become intimately fused together, but some characters refuse to blend, and are transmitted in an unmodified state, either from both parents or from one (1c, 2:67).

As cases in point, Darwin cites the crossing of gray and white mice, the offspring being pure white or gray, but not intermediate, and the crossing of white, black and fawn-colored Angora rabbits, in which the colors are separately inherited, and not combined in the same animal. The non-intermediate character of the inheritance in the case of turnspit dogs and ancon sheep is referred to, as is also the inheritance in the case of tail-less, horn-less breeds. Similar results in the case of stocks, toad-flax and sweet peas are cited (1b, p. 68).

Darwin (1c, 44–45), in discussing what he called "prepotency," was dealing in very many cases with that which we now recognize as simple dominance. For example, in the crossing of snap-dragons, Darwin found that when the normal or irregular-flowered type was crossed with the abnormal or regular-flowered type, the former prevails in the first generation to the exclusion of the latter. These 127 hybrid plants self-fertilized, yielded in the second generation irregular to regular plants in the ratio of 88 to 37. This is very close to the exact 3:1 ratio which would be represented by the numbers 85:42. Darwin, however, simply regards it as a

> good instance of the wide difference between the inheritance of a character and the power of transmitting it to the crossed offspring (1b, 45).

Darwin was thus quite unable, with the information then available, to frame a satisfactory explanation for the various phenomena passing under the name of "prepotency."

He makes one remark relative to prepotency, however, that slightly grazes the present-day presence and absence theory of Mendelian inheritance.

> We can seldom tell what makes one race or species prepotent over another; but it sometimes depends on the same character being present and visible in one parent, and latent or potentially present in the other (1c, 2:58).

The matter of sex-linked characters did not escape Darwin's observation, alluding to cases where a son does not inherit a character directly from his father, or transmit it directly to his son, but receives it by transmission from a mother who does not show it, and transmits it through his non-affected daughter. Darwin observes:

> We thus learn that transmission and development are distinct powers (*ibid.*).

Respecting the matter of reversion, or what we should now call recombination after segregation, Darwin's utterances are remarkable, especially in "Animals and Plants under Domestication." In most cases he regards "reversion" as the coming to light of a "latent" character, as, e. g.,

> hornless breeds of cattle possess a latent capacity to reproduce horns, yet when crossed with horned breeds they do not invariably produce offspring bearing horns (1c, 2:44).

Darwin deserves credit for strictly contesting the point of view then widely current, that the longer a character is handed down by a breed, the more fully it will be continued in transmission. Discussing some of the cases, he says (1c, 2:37):

> In none of these nor in the following cases, does there appear to be any relation between the force with which a character is transmitted and the length of time during which it has been transmitted.

The basis for such a view, that the longer a breed is handled and the more it is selected, the more homozygous it becomes, was not scientifically known in Darwin's time, but Darwin actually perceived that the mere repeated act of selection itself, whatever else might be involved, would not increase the potency of transmission, or eliminate beyond question the liability to reversion.

Darwin considered it doubtful whether, as was then popularly supposed, the length of time during which a character had been inherited, had any influence on its fixedness, and concluded from the fact that when wild species which have remained so for ages, are brought into cultivation, they immediately begin to vary, that no character by long inheritance can be considered as absolutely fixed (1c, 2:56).

In this work, more than elsewhere, Darwin devoted himself particularly to the question of the meaning of inheritance in hybrids. The question always demanding explanation was the reason for the reappearance after the first generation of a hybrid of a parental, or even of an ancestral form, a phenomenon then called "reversion," including, as Darwin says:

> all cases in which an individual with some distinguishable character, a race or species, has, at some former period been crossed, and a character derived from his cross, after having disappeared during one or several generations, suddenly reappears (1c, 2:2).

Darwin, at the outset, merely comments on the result of crossing as follows:

> In considering the final result of the commingling of two or more breeds, we must not forget that the act of crossing in itself tends to bring back long-lost characters not proper to the immediate parent form (1c, 2:64).

It was noticed that from three to eight generations were usually required before a breed derived from a cross comes to be considered free from danger of reversion. What constituted the machinery to bring about reversion remained, but for Mendel's as yet undiscovered researches, absolutely unknown. The state of knowledge in that regard is well exemplified by Darwin's remark,

> That the act of crossing in itself gives an impulse towards reversion, as shown by the reappearance of long-lost characters, has never, I believe been hitherto proved (1c, 2:13).

Darwin recognized, as did most of the breeders before Mendel, that

> As a general rule, crossed offspring in the first generation are nearly intermediate between their parents, but the grandchildren and succeeding generations continually revert in a greater or lesser degree, to one or both of their progenitors (1c, 2:22).

From cases of intermediacy, Darwin proceeds to discuss what we should call cases of dominance, and finally cases in which the offspring in the first generation are neither intermediate nor uni-parental in type, but in which there is vegetative splitting, or somatic segregation:

> In which differently colored flowers borne on the same root resemble both parents, . . . and those in which the same flower or fruit is striped or blotched with the two parental colors, or bears a single stripe of the color or other characteristic quality of one of the parent forms (1c, 2:69).

It is interesting to see how Darwin now undertook, in the absence of experimental evidence, to devise a scientific solution for the reappearance of parental characters in the second generation of the offspring. Taking Naudin's idea of segregation or "disjunction" of the elements of the species, he concludes as follows:

> If . . . pollen which included the elements of one species happened to unite with ovules including the elements of the other species, the *intermediate or hybrid state would still be retained, and there would be no reversion.* But it would, as I suspect, be more *correct to say that the elements of both parent species exist in every hybrid in a double* state, namely, blended together and completely separated (1c, 2:23).

The above paragraph comes more nearly being a statement of the true nature of the hybrid or heterozygote condition as Mendel's analysis has revealed it, than any other account hitherto published.

Combining this with the following statements, we have very nearly the same idea which Mendel's theory involves, based, however, upon Darwin's theory of pangenesis, whereby each cell was supposed to throw off "gemmules" which carried the characters to the reproductive cells. He says:

> The tendency to reversion is often induced by a change of conditions, and in the plainest manner by crossing. Crossed forms of the first generation are generally nearly intermediate in character between their two parents, but in the next generation the offspring commonly revert to one or both of their grandparents, and occasionally to more remote ancestors (1c, 2: 383).

Darwin then assumes that in the hybrid there exist two kinds of "gemmules" or character-carriers; viz., pure gemmules from each of the two parent forms, and combined or hybridized gemmules as well, and proceeds in the following statement, to give about as clear an account as we have to-day, of the cause for the reappearance of the parental or homozygote forms.

> . . . *when two hybrids pair, the combination of pure gemmules derived from the one hybrid with the pure gemmules of the same parts derived from the other would necessarily lead to complete reversion of character,* and it is perhaps not too bold a supposition that unmodified and undeteriorated gemmules of the same nature would be especially apt to combine.
>
> Pure gemmules in combination with hybridized gemmules would lead to partial reversion, and lastly, *hybridized gemmules derived from both parent-hybrids, would simply reproduce the original hybrid form.* All these cases and degrees of reversion incessantly occur (1c, 2: 383).

The latter statement is virtually a statement of the condition of things in heterozygosis, in principle as we have it to-day. If we assume the "hybridized" gemmules to represent the "*Dr.*" combination, we have the necessary substitution.

Darwin's theory was a natural corrollary to his doctrine of pangenesis. It seems strange that with Naudin's idea of disjunction in hand, and with the phenomenon of segregation in peas, noticed by five observers, all of whose experiments Darwin remarks upon, that Darwin did not himself perform Mendel's experiment. However, it is a manner of special interest that *à priori,* in the absence of experimental data, he should have come as near the principle of the Mendelian explanation as the above passages indicate.

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